BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. 15 September, 1969 Number 324

POLYMORPHISM AND EVOLUTION OF THE HISPANIOLAN SNAKE GENUS *UROMACER* (COLUBRIDAE)

Henry S. Horn[1]

Abstract. Four species of the endemic genus *Uromacer* are recognized: *catesbyi, frenatus, oxyrhynchus,* and *dorsalis.* All save *dorsalis* show a remarkably discrete di- or trimorphism in a color pattern that is apparently cryptic. The adaptive significance of this polymorphism is discussed using an intuitive model that draws on the theory of Levins.

The species are linearly ordered on the basis of body shape. Surprisingly, the stomachs of the stoutest species contain arboreal lizards and frogs, while the slimmer species take progressively more terrestrial lizards. The linear order suggests a pattern of geographic speciation occurring at the time when the northern and southern portions of Hispaniola were separate islands. Thus the pattern is consistent with patterns of evolution and migration proposed for other Hispaniolan reptiles by Williams and others. Speculations about the origin of *dorsalis,* endemic to Île de la Gonâve, may explain why the fauna of that islet is a curious mixture of species characteristic of the northern and southern portions of Hispaniola.

INTRODUCTION

The snakes of the genus *Uromacer* are endemic to Hispaniola and the surrounding islets. Some years ago A. Stanley Rand discovered a color polymorphism in several local populations of *Uromacer oxyrhynchus.* Examination of the other species has shown that several of them are also polymorphic. Since the same morphs of different species are superficially more similar than are different morphs of the same species, this polymorphism sometimes results in the misidentification of museum specimens. Consequently, the polymorphism has obscured the pattern of distribution of the forms of *Uromacer*, making it difficult to relate their distribution to that of other Hispaniolan reptiles.

---

[1] Department of Biology, Princeton University, Princeton, New Jersey.

The recent concentration on the herpetology of Hispaniola at the Museum of Comparative Zoology (MCZ) has provided large, synchronous collections of *Uromacer* from several localities. The geographical coverage of even these large collections is not yet extensive enough to warrant a definitive discussion of intraspecific variation. However, the available collections allow me to assess the validity of the described species of *Uromacer*, to suggest the pattern of their relationships, to document their striking polymorphism in some detail, and to comment on some interesting evolutionary problems posed by the genus. Though I have studied only preserved material, I have made inferences about the ecology of the species from their stomach contents. However, I must leave several questions unanswered because I lack field knowledge of Hispaniola, particularly of seasonal changes during the year.

Where MCZ material was insufficient, I have examined specimens from the American Museum of Natural History (AMNH), the British Museum (Natural History) (BMNH), the Field Museum of Natural History (FMNH), the Yale Peabody Museum (YPM), the Albert Schwartz Field Series (ASFS), and the United States National Museum (USNM). I am grateful to the curators of these collections for allowing me to examine specimens in their charge.

I thank A. Stanley Rand and Ernest E. Williams for discussion and criticism throughout this study. Dr. Rand introduced me to *Uromacer*, and his unpublished notes on their polymorphism were the starting point for my work. Dr. Williams sponsored part of this study as my undergraduate thesis at Harvard College in 1962. My ideas on polymorphism developed from discussions with Richard Levins and Robert H. MacArthur. For criticisms of several manuscripts, I am indebted to Thomas H. Frazzetta, Elizabeth G. Horn, Thomas W. Schoener, Albert Schwartz, and George G. Simpson. Dr. Schwartz kindly compiled the faunal list for Île de la Gonâve.

MATERIAL AND METHODS

Cochran (1941) recognized six species of *Uromacer: catesbyi, scandax, frenatus, wetmorei, dorsalis,* and *oxyrhynchus.* There is reason to doubt the specific distinctness of *scandax* and *wetmorei*, which Cochran recognized as respectively allied to *catesbyi* and *frenatus.* For reasons given in the Appendix, I consider *scandax*

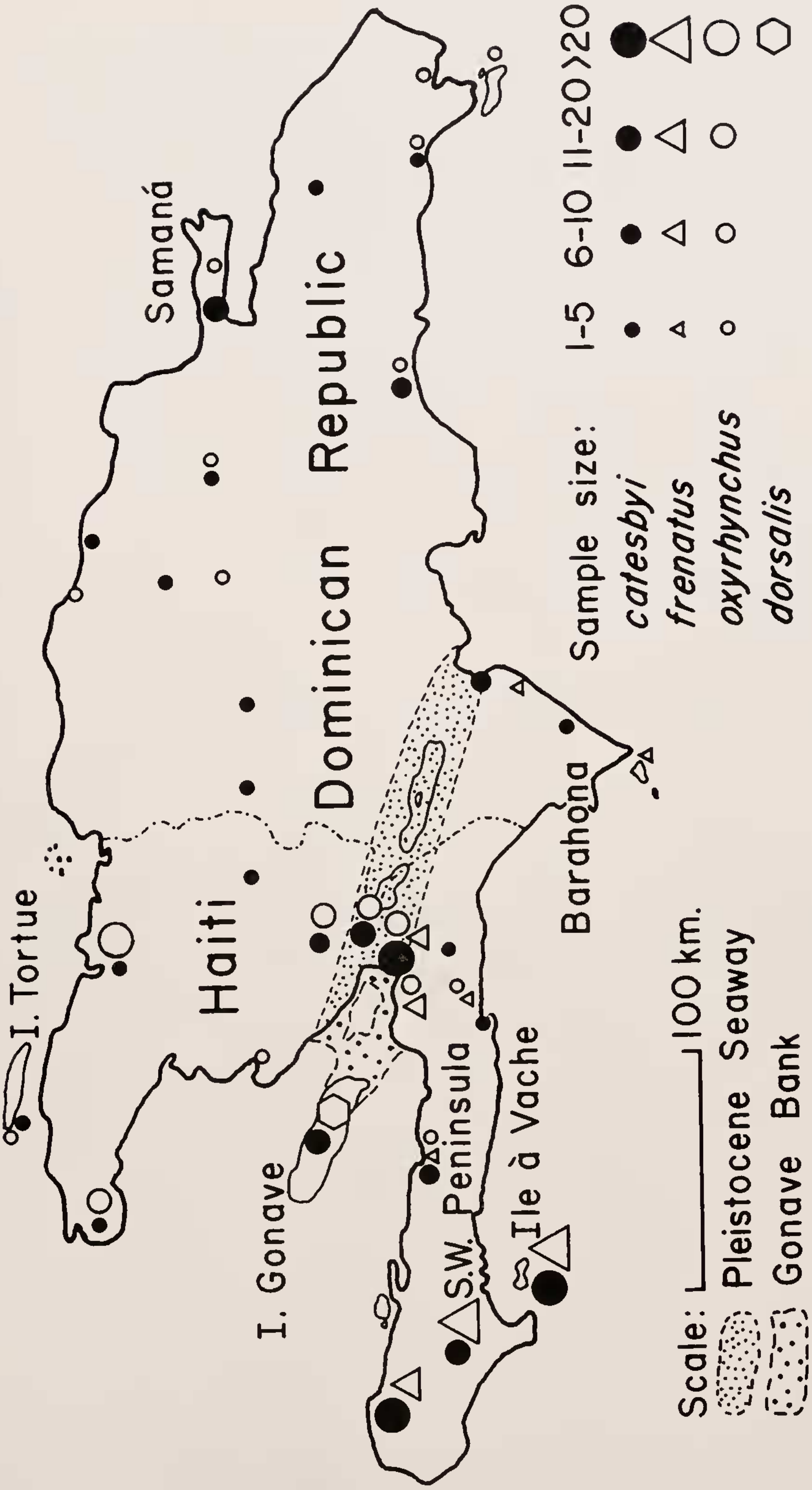

Figure 1. Hispaniola, showing locality records for *Uromacer*.

to be identical with *catesbyi*, and *wetmorei* to be a subspecies of *frenatus*. The remaining species are easily separated by the diagnostic characters of Cochran's key: snout length relative to eye diameter, ventral scale count, and midbody scale rows. The ranges of snout length and ventral scale count overlap between species, but these characters are usually sufficient for tentative identification of single specimens. The number of scale rows at midbody is constant in each species, but is diagnostic only for *oxyrhynchus*. The subcaudal scale count for each species has a large range, and though there may be significant differences between the means of different populations, it is seldom useful in identifying a single specimen. Similarly, the presence or absence of an anterior loreal may be used to infer relationships among populations, but it is useless as a diagnostic character.

Stomach contents of the MCZ and YPM specimens were removed and identified. The snakes had fed primarily on *Anolis* whose ecology is relatively well known, so inferences about the ecology of *Uromacer* may be made on the basis of these stomach contents. Schwartz (in litt.) and Mertens (1939) have observed that freshly caught *Uromacer* often swallow the cohabitants of a collecting bag, but even those stomach contents that were not eaten by free snakes will reflect the syntopic fauna in which the snakes were collected. To minimize this difficulty, those stomach contents that were undigested were ignored in analysis.

Where different color morphs are described for a single species of *Uromacer*, these morphs are entirely distinct, with no intermediates except between the gray and the striped gray forms. There was never any hesitation in assigning any well-preserved specimen to one of three alternative morphs: *green*, green above and below, lighter below; *gray-green*, green above, mottled gray below; or *gray*, gray above and below. A detailed description of each morph and its variations in each species is given in the Appendix.

RESULTS AND INTERPRETATIONS

The ranges of the species of *Uromacer* are mapped in Figure 1 and listed in Table 1.

External metric characters are listed in Table 2, and there are photographs of the several species in Figure 2. The species may be linearly ordered, as in the table, on the basis of characters that are correlated with slimming and lengthening the body. *U. catesbyi* is typically colubrid in shape, with a short, blunt snout, low

TABLE 1

Ranges of the species of *Uromacer*

Species	*Southwest and Barahona Peninsulas*	*Port-au-Prince and vicinity*	*N. and E. Dominican Republic*	*Île de la Gonâve*
catesbyi	*	*	*	*
frenatus	*	*		
oxyrhynchus		*	*	?
dorsalis				*

TABLE 2

Metric morphology of the species of *Uromacer*

Species	*Number examined*	*Snout length relative to eye diameter*	*Ventral scales*	*Subcaudal scales*	*Scale rows at midbody*	*Anterior loreal*
catesbyi	254	2.0	167 ±0.7	183 ±1.0	17	—
		*	*	*		
frenatus	102	2.6	187 ±0.5	204 ±1.9	17	—
		*	*		*	*
oxyrhynchus	129	3.0	200 ±0.5	199 ±1.1	19	present in 25
				*	*	*
dorsalis	84	2.9	200 ±1.2	210 ±2.2	17	+

Entries are the means for each character ± the standard error of the mean. The standard error of the mean snout length (±0.01) was, in all cases, less than the reading error of each measurement (±0.2). Numbers separated by * are significantly different at the .05 level by a one-tailed *t* test (Snedecor, 1956), for snout length, ventral count, and subcaudal count, or a binomial test (Siegel, 1956), for scale rows at midbody and anterior loreal.

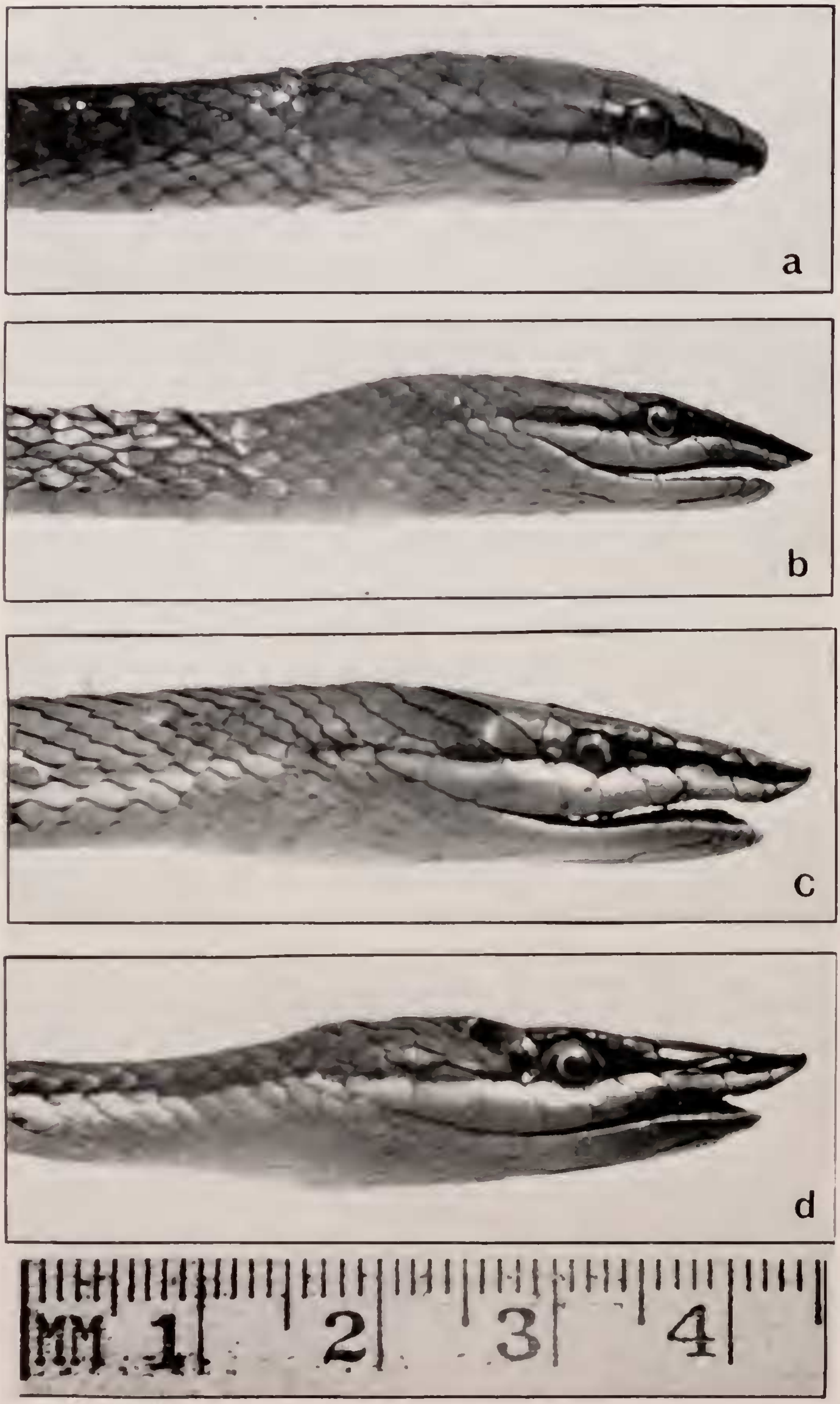
a
b
c
d
MM 1
2
3
4

Figure 2. a, *Uromacer catesbyi* MCZ 57764 nr. Carpintero, Dominican Republic; b, *U. frenatus* MCZ 65530 Perrine nr. Jérémie, Haiti; c, *U. oxyrhynchus* MCZ 62713 Bombardopolis, Haiti; d, *U. dorsalis* MCZ 80815 Pointe-à-Raquettes, Île de la Gonâve, Haiti.

ventral and subcaudal counts, and a relatively thick body covered with rhomboidal scales that are nearly square. *U. oxyrhynchus* and *dorsalis* are shaped more like typical tree and vine snakes, with long, pointed snouts, high ventral and subcaudal counts, and more slender bodies covered with obliquely rhomboidal scales. *U. frenatus* is intermediate between these extremes.

The stomach contents of *Uromacer* are listed in Tables 3 and 3a. In Table 3 the stomach contents of the snakes are pooled within

TABLE 3

Habitat of food taken by the species of *Uromacer*

Habitat	*catesbyi*	*frenatus*	*oxyrhynchus*	*dorsalis*
Trees	7	3	1	2
Tree trunks and bushes	9	5	11	4
Grass and open areas		2	4	11
Ground and rocks		4	4	10

TABLE 3a

Stomach contents of the species of *Uromacer*

Habitat and species eaten	*catesbyi*	*frenatus*	*oxyrhynchus*	*dorsalis*
TREES				
Hyla pulchrilineata	1			
dominicensis	3			
Anolis chlorocyanus	2		1	2
coelestinus	1	3		
TREE TRUNKS & BUSHES				
Anolis cybotes	4	4	8	3
brevirostris				1
distichus	5	1	3	
GRASS & OPEN AREAS				
Anolis semilineatus		2	3	
olssoni			1	11
GROUND & ROCKS				
Ameiva taeniura		1	2	1
chrysolaema				6
Leiocephalus melanochlorus		2		
vinculum				3
schreibersii			2	
Sphaerodactylus sp.		1		

common habitats of the food species; the habitat groupings were made by referring to Mertens (1939), Williams and Rand (1961), and Rand (1962). Since the groupings are only generalizations, and the samples are small and heterogeneous, the data do not fully characterize the diets of the species of *Uromacer*. However, the differences among the diets are so striking, when compared to the uniformity of diets within each species, that crude relative characterizations can be made with confidence.

U. catesbyi takes arboreal food almost exclusively, and *dorsalis* feeds primarily on terrestrial food, whereas *f. frenatus* and *oxyrhynchus* are intermediate and more similar to each other than either is to *catesbyi*. The tendency for the colubrid-like *catesbyi* to take arboreal prey, and for the longer-snouted species to take progressively greater proportions of terrestrial prey, is the opposite of expectations based on the morphology of the species (e.g. Mertens, 1939, who suggest that *oxyrhynchus* is the most arboreal species of *Uromacer*).

Polymorphism. Of the four species of *Uromacer,* only the gray *dorsalis* is not demonstrably polymorphic in at least one locality (see Table 4). Green *U. catesbyi* occur throughout the range of the species, but with a pattern unlike the corresponding morph of any other species; *catesbyi* is polymorphic, with a gray form, near Miragoâne, in the middle of the southwest peninsula of Haiti.

TABLE 4

Distribution of the color morphs of the species of *Uromacer*

Species	*Green*	*Gray-green*	*Gray*	*Gray (striped)*
catesbyi	ENTIRE RANGE		Miragoâne	
f. frenatus		Ile à Vache	mainland	Île à Vache
f. wetmorei		Barahona		Isla Beata
oxyrhynchus	ENTIRE RANGE	Haiti & Eastern D.R.	Haiti	
dorsalis				ENTIRE RANGE

U. f. frenatus is monomorphic gray on the mainland, and polymorphic gray and gray-green on Île à Vache. The gray form on Île à Vache resembles that of *dorsalis* more than that of mainland *frenatus* or *oxyrhynchus*. *U. f. wetmorei* on Barahona may be polymorphic, but the few poorly-preserved specimens presently available from scattered localities are insufficient evidence.

U. oxyrhynchus is apparently monomorphic green through much of the Dominican Republic, but it is dimorphic green and gray-green throughout the Haitian portion of its range. In scattered Haitian localities it is trimorphic, green, gray-green, and gray. *U. oxyrhynchus* may in fact be trimorphic throughout the Haitian portion of its range, perhaps in parts of the Dominican Republic as well. The gray morphs are rare enough to be found only in large, synchronous collections from Haiti; no such collections have been made in the Dominican Republic.

The discreteness of the morphs in all the polymorphic species, and the lack of intermediates, suggests that the mechanism controlling the polymorphism is an allelic switch at a single genetic locus. In the trimorphic *oxyrhynchus*, the distribution of the morphs is consistent with the interpretation that the green and the gray forms are homozygotes and that the commoner gray-green form is the heterozygote; i.e. in all the localities from which both green and gray specimens have been taken, gray-green specimens have been taken as well.

The distribution of the color forms among the localities of the polymorphic species and among the species of the genus suggests that the various forms are cryptic for different surroundings. *U. catesbyi* is green throughout its range, darker in the western portions of Hispaniola than in the eastern, with some gray individuals on the southwest peninsula in the Miragoâne area. *U. frenatus* is gray on the southwest peninsula and polymorphic on Île à Vache, while its ecological counterpart, *oxyrhynchus*, has green, gray-green, and gray morphs in Haiti, but a preponderance of green morphs in the Dominican Republic (see Table 5). These distributions correspond roughly to the pattern of humidity and vegetation on Hispaniola, as described by Wetmore and Swales (1931: 2-7).

TABLE 5

Geographical distribution of the color morphs of *frenatus* and *oxyrhynchus*

Species	*Area*	*Green*	*Gray-green*	*Gray*
f. frenatus	Île à Vache		15	22
f. frenatus	Haitian mainland		2	56
f. wetmorei	Barahona		4	1
oxyrhynchus	Haiti	47	48	4
oxyrhynchus	Dominican Republic	17	4	

The grayer and darker (i.e. less bright green) forms are associated with the drier, western portion of the island. The presence of the gray-green morph of *frenatus* on Île à Vache and the brighter green of the *catesbyi* from the islet are correlated with the presence of denser woodland on the islet than on the adjacent mainland. This correlation of the distribution of the color morphs with foliage density suggests cryptic coloration as a possible function of the different morphs.

The two most strictly monomorphic species, *catesbyi* and *dorsalis,* are characterized by the most restricted diets. The green *catesbyi* takes only arboreal prey, while the gray *dorsalis* takes predominantly terrestrial prey. This additional correlation of color pattern with ecology suggests again that the coloration of *Uromacer* is cryptic, concealing the snake as it stalks agile prey.

Polymorphism in a cryptic pattern of coloration poses an interesting evolutionary question. If a specific color pattern is indeed cryptic, why is more than one pattern present at all? The theory of polymorphism provides some likely answers and suggests the kinds of data that should be sought to choose between alternatives. Levins (1962-6; Levins and MacArthur, 1966) has examined the adaptive significance of polymorphism, using an abstract mathematical model of extreme generality. I shall develop a much simpler model to examine polymorphism in the special case of cryptic coloration, but the intellectual basis and results are the same as those of Levins. This model is almost absurdly simple, but the concepts illustrated are quite general and are not easily apparent without the model.

The environment is a checkerboard with black and white squares and the cryptic animals are checkers. Later I shall introduce reproduction and "fitness" into the model, but first let us look at crypticity alone. If we randomly place black or white checkers on the squares of the checkerboard, roughly half the black checkers will fall on black squares and half the white checkers, on white. Thus half the population of either black or white checkers will be cryptic. However, if we throw gray checkers on the checkerboard, none of them will be cryptic, unless, of course, the checkers are very large and the squares of the checkerboard are so tiny that it looks like the gray of a halftone illustration. Thus if two alternative morphs are to be cryptic, the environment must be a mixture of large patches of different kinds, each with an extreme morph that is more cryptic than an intermediate morph.

I assume that "adaptation" is achieved through natural selection, which favors that individual whose offspring form the greatest proportion of breeders in the next generation. Correspondingly the "fitness" of an individual is defined as the number of his offspring that breed in the next generation, and the individual with the greatest fitness in a given environment is the "best adapted" to that environment.

We now allow each checker to reproduce an average of X offspring in each generation; in each reproductive period we throw checkers onto the board and give each checker X+d offspring if it is cryptic but only X−d offspring if it is not cryptic. Black checkers have black offspring; white checkers have white offspring. We define "polymorphic" checkers to have either black or white offspring with a 50-50 chance, whether the phenotype of the "polymorphic" checker is black or white. The genetic or developmental basis of this polymorphism need not be specified, so I shall call it "sibling polymorphism," since it requires that the offspring of a given morph may include both morphs. If the checkerboard has an equal number of black and white squares, then the offspring of black, white, or polymorphic checkers have an equal chance of being cryptic or non-cryptic, and the fitness of each type is an average of X+d and X−d, or simply X. (You can easily show that if the environment is an uneven mixture of black and white squares, the morph that is cryptic in the commoner square has a higher fitness than the other morph or the polymorph.) Thus, if the environment is a spatial mixture of large patches of two types, a monomorphic population is better adapted than a polymorphic population, or at least as well adapted.

If, instead of throwing the checkers onto the board randomly, we allow each of the checkers to choose and reproduce in its appropriate habitat, then the white squares will be occupied predominantly by white checkers and the black squares by black checkers. On sampling a large and heterogeneous area, we then obtain both morphs, and the population appears to be polymorphic. However, the two morphs could represent two species, rather than a polymorphic species. In fact, the average fitness of individuals of the two separate species would be higher than that of a polymorphic species, unless the polymorphism continually adjusted the ratio of the morphs to match the proportions of the corresponding patches in the environment. Since this polymorphism may result from sampling a heterogeneous environment and does not require that a given individual be capable of having polymorphic offspring, I shall call it "sampling polymorphism" as distinct from "sibling polymorphism." (Under certain restricted conditions the two kinds of polymorphism are convergent, and sampling polymorphism may evolve a genetic basis. See Levins, 1965, for a discussion.)

Now instead of throwing the checkers onto a checkerboard, we throw them alternately onto a white board or a black board for each generation. That is, the environment is a temporal mixture of different habitats, rather than a spatial mixture. The black and white checkers are alternately cryptic and non-cryptic. Each individual in a cryptic generation has $X+d$ offspring, each of whom has $X-d$ offspring in the next generation; thus the average fitness of black or white checkers over two generations is $(X+d)(X-d) = X^2-d^2$. On the other hand, the "polymorphic" checkers have an equal number of cryptic and non-cryptic offspring in each generation and their average fitness is $\frac{1}{2}(X+d)+\frac{1}{2}(X-d) = X$ in each generation; then the average fitness of polymorphic checkers over two generations is X^2, which is always greater than X^2-d^2. If the black and white environments alternate several times within each generation, fitness is averaged over the two environments for each generation, and the results are the same as in the case of spatial heterogeneity. However, sibling polymorphism yields a higher average fitness than monomorphism when the environment varies drastically with a period of the same order of magnitude as the time between generations.

What does the checkerboard model predict about *Uromacer*? If the polymorphism of *Uromacer* is simply a sampling polymorphism, then the different morphs should be associated with distinctly different habitats or microhabitats. The habitats might be different types of vegetation, in each of which one of the morphs is most cryptic.

If the polymorphism of *Uromacer* is a sibling polymorphism, the alternative morphs should still be cryptic in distinctly different habitats, but the habitats will alternate in an inescapable temporal pattern, e.g. wet-dry season. Therefore, if the polymorphism is a genetic or developmental adaptation to a temporally heterogeneous environment, the different morphs will often be found in habitats in which they are not cryptic.

Documenting the adaptive significance of polymorphism in *Uromacer* is a difficult, long-term project. It is first of all a field, not a museum project. It is necessary to define the habitats in which each of the morphs is most cryptic. Then the alternatives of genetic and sampling polymorphism must be separated by determining the distribution of the morphs among the several habitats, over a time equal to several generations of *Uromacer*. As interesting as the problem is, it will probably not be quickly solved, perhaps not even quickly undertaken, since the required study is longer than the lifetime of the average research grant.

Relationships within the genus. There has been no previous discussion of the relationships of the species of *Uromacer*.

It is at once tempting to suggest that the morphological and dietary series described corresponds to an evolutionary series as well; that *catesbyi* is the most primitive of the *Uromacer*, *oxyrhynchus* and *dorsalis* the most recently derived, and that *frenatus* represents an intermediate step. When the present ranges of the species, the physiographic history of Hispaniola, and the mechanisms of geographic speciation are taken into account, this suggestion is strengthened.

During the Pleistocene, Hispaniola was divided by an arm of the sea into two large islands, a northern island, Haiti north of the Cul-de-Sac Plain and the Dominican Republic exclusive of the Barahona peninsula, and a southern island, the southwest peninsula of Haiti and the Barahona peninsula (Schuchert, 1935; Weyl, 1966; Williams, 1961). The ancestral colubrid (Maglio, in prep., suggests something similar to *Alsophis*) had given rise to a *catesbyi*-like form, to be called "proto-catesbyi," and to "proto-frenatus," autochthons of the northern and southern islands respectively. Proto-frenatus invaded the northern island, and as it came into contact with the well-established proto-catesbyi, the characteristics that distinguished the two species were intensified (character divergence of Mayr, 1963, after Darwin). By its increased divergence from proto-catesbyi, the invading proto-frenatus gave rise to "proto-oxyrhynchus," ancestor of *oxyrhynchus* and *dorsalis*.

The proposed sequence accounts for the presence in *dorsalis* of characters similar to both *frenatus* and *oxyrhynchus*. The progenitor of *dorsalis* on Gonâve was presumably proto-oxyrhynchus, which would have retained similarities to proto-frenatus and thus to *frenatus*, while differentiating in the direction of *oxyrhynchus*. Alternatively, *dorsalis* could have been derived directly from proto-frenatus, and its similarity to *oxyrhynchus* could represent parallel evolution of the species. Lack of evidence relevant to these alternatives is in itself sufficient reason for provisionally calling *dorsalis* a separate species.

This evolutionary sequence is only an interpretive hypothesis and cannot be tested, but it embodies processes that have been suggested to account for the present distribution of other Hispaniolan reptiles. The postulated distinction of proto-catesbyi and proto-frenatus, as the respective autochthons of the northern and southern islands, is paralleled by the distinction of *Anolis coelestinus* and *Anolis chlorocyanus,* of *Anolis aliniger* and *Anolis singularis,* and perhaps of the *Anolis* of the *monticola* group and the subspecies of *Anolis ricordii* (Thomas and Schwartz, 1967; Williams 1965a, 1965b). The subsequent invasion of the northern island by proto-frenatus is paralleled by the *Anolis* of the *semilineatus* group. Williams (1961) suggests that *Anolis olssoni* and *A. semilineatus* are indigenous to the northern and southern islands respectively and that their present distributions are the result of the relatively recent invasion of the northern land mass by *semilineatus.* Similarly, Schwartz (1967) suggests that *Ameiva taeniura* originated on the southern island and has since invaded the northern land mass.

There are probably other patterns of radiation that are consistent with the present ranges of the species of *Uromacer,* and almost as simple in the changes of morphology that they would require. However, several conclusions will remain unchanged given such alternative patterns. *U. catesbyi* is clearly more different, in morphology and diet, from the other species than they are from one another. It is then significant that only *catesbyi* is broadly sympatric with the other species of the genus. *U. frenatus, oxyrhynchus,* and *dorsalis* are similar in morphology and may provisionally be considered allopatric ecological replacements.

Explaining the origin of *dorsalis* on Gonâve as more than a historical accident requires bold speculation in the absence of critical data. This speculation is justified, however, as it also suggests a possible derivation for the problematical fauna of Gonâve.

Present knowledge of the fauna of Gonâve is scanty, but it is already apparent that the fauna is an odd mixture of species characteristic of the northern and southern islands of the Pleistocene (See Table 6). During part of the Pleistocene, Gonâve was reduced to about one fourth of its present area (Butterlin, 1960). When the northern and southern islands were rejoined, Gonâve may have been connected to the mainland by a spit at least 3 km wide to the north and 7 km wide to the south (Fig. 1; also Woodring et al., 1924), which would have allowed the fauna of both regions to invade Gonâve. When Gonâve became insular again, those species whose presence had depended on continuing invasion would be eliminated, leaving only those best adapted to the restricted habitats of Gonâve and those potential competitors that were most divergent. The geographic origin of the invading species would be irrelevant to their subsequent persistence.

TABLE 6

Reptiles of Gonâve and their areas of origin

Species	*Origin*[1]	*Reference*
Gonatodes albogularis		
Sphaerodactylus cinereus		
Aristelliger cochranae		
Anolis brevirostris (end. subsp.)		
chlorocyanus	North	Williams, 1965a
cybotes		
olsoni	North	Williams, 1961
singularis	South	Williams, 1965a
Cyclura cornuta		
Leiocephalus vinculum (end. subsp.)		
Ameiva chrysolaema (end. subsp.)	North	Schwartz & Klinikowski, 1966
taeniura	South[2]	Schwartz, 1967
Diploglossus curtissi		
Amphisbaena gonavensis (end. subsp.)	South?	Thomas, 1965
Typhlops capitulatus (end. subsp.)		
pusillus	North	Richmond, 1964
Epicrates angulifer		
fordi		
Tropidophis haetianus		
Dromicus parvifrons		
Hypsirhynchus ferox		
Ialtris dorsalis		
Uromacer catesbyi	North[2]	
dorsalis (endemic)	North	

[1] North and south under this heading refer to the northern and southern islands into which Hispaniola was periodically divided during the Pleistocene. See Fig. 1.

[2] Island of origin of parent species, though invasion may have been from a population on the other island.

In particular, if proto-catesbyi, proto-frenatus, and proto-oxyrhynchus all reached peninsular Gonâve, the ultimate persistence of the most divergent pair, and the elimination of the intermediate proto-frenatus is predictable. The dietary divergence of *dorsalis* and *catesbyi* confirms the role of interspecific competition in the origin of *dorsalis*. *U. dorsalis* clearly differs from *catesbyi* in foraging habitat, if not in foraging behavior, to a greater extent than *frenatus* and *oxyrhynchus* differ from *catesbyi* (Table 3). Interspecific competition may necessitate this increased divergence of *dorsalis* and *catesbyi* on Gonâve, whereas less divergence insures the coexistence of two sympatric *Uromacer* on the more extensive and heterogeneous Haitian mainland.

If the history above is wrong, Gonâve deserves intensive study as an extraordinary example of an island colonized from two comparable and equidistant sources. If the suggested history is correct, then Gonâve is a model of the faunal transformations of a continental island that when peninsular had the full complement of species of the adjacent mainland: while several closely related species could persist when immigration from the mainland was easy, fewer were able to persist after their populations became insular. Those that did persist on the island had to be strongly divergent ecologically. According to such a model, an interpretation of the fauna of a continental island must emphasize the ecological compatibilities of the potentially resident species, rather than their relative vagilities and routes of invasion from the adjacent mainland.

LITERATURE CITED

Butterlin, J.
1960. Géologie générale et régionale de la République d'Haiti. Travaux et Mémoires de l'Institut des Hautes Etudes de l'Amérique Latine, Paris, **6**, 194 pp.

Cochran, D.
1931. New reptiles from Beata Island, Dominican Republic. Proc. Biol. Soc. Washington, **44**: 89-92.
1941. The herpetology of Hispaniola. Bull. U.S. Nat. Mus., **177**: 1-398.

Dunn, E. R.
1920. On the Haitian snakes of the genera *Leimadophis* and *Uromacer*. Proc. New England Zool. Club, **7**: 37-44.

Levins, R.
1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. Amer. Nat., **96**: 361-373.

1963. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. Amer. Nat., **97**: 75-90.

1964. Theory of fitness in a heterogeneous environment. III. The response to selection. J. Theoret. Biol., **7**: 224-240.

1965. Theory of fitness in a heterogeneous environment. IV. The adaptive significance of gene flow. Evolution. **18**: 635-638.

1966. The strategy of model building in population biology. Amer. Sci., **54**: 421-431.

Levins, R., and R. H. MacArthur

1966. The maintenance of genetic polymorphism in a spatially heterogeneous environment: variations on a theme by Howard Levene. Amer. Nat., **100**: 585-589.

Mayr, E.

1963. Animal Species and Evolution. Cambridge, Mass., Belknap Press, Harvard University Press, 797 pp.

Mertens, R.

1939. Herpetologische Ergebnisse einer reise nach der Insel Hispaniola, Westindien. Abh. Senckenberg. Naturf. Ges., **449**: 1-84.

Rand, A. S.

1962. Notes on Hispaniolan herpetology. 5. The natural history of three sympatric species of *Anolis*. Breviora, Mus. Comp. Zool., No. **154**: 1-15.

Richmond, N. D.

1964. The blind snakes (*Typhlops*) of Haiti with descriptions of three new species. Breviora, Mus. Comp. Zool., No. **202**: 1-12.

Schuchert, C.

1935. Historical Geology of the Antillean-Caribbean Region. New York, John Wiley & Sons. 811 pp.

Schwartz, A.

1965. The *Leiocephalus* (Lacertilia, Iguanidae) of Hispaniola. I. *Leiocephalus melanochlorus* Cope. Journ. Ohio Herp. Soc., **5**: 39-48.

1967. The *Ameiva* (Lacertilia, Teiidae) of Hispaniola. III. *Ameiva taeniura* Cope. Bull. Mus. Comp. Zool., **135**: 345-375.

Schwartz, A., and R. F. Klinikowski

1966. The *Ameiva* (Lacertilia, Teiidae) of Hispaniola. II. Geographic variation in *Ameiva chrysolaema* Cope. Bull. Mus. Comp. Zool., **133**: 427-487.

Siegel, S.

1956. Nonparametric Statistics for the Behavioral Sciences. New York, McGraw-Hill, 312 pp.

Snedecor, G .W.

1956. Statistical Methods Applied to Experiments in Agriculture and Biology. Ames, Iowa, Iowa State Univ. Press, 534 pp.

Thomas, R.

1965. Two new subspecies of *Amphisbaena* (Amphisbaenia, Reptilia) from the Barahona Peninsula of Hispaniola. Breviora, Mus. Comp. Zool., No. **215**: 1-14.

THOMAS, R., AND A. SCHWARTZ
1967. The *monticola* group of the lizard genus *Anolis* in Hispaniola. Breviora, Mus. Comp. Zool., No. **261**: 1-27.

WETMORE, A., AND B. H. SWALES
1931. The birds of Haiti and the Dominican Republic. Bull. U.S. Nat. Mus., **155**: 1-483.

WEYL, R.
1966. Geologie der Antillien. Beiträge zur Regionalen Geologie der Erde, Vol. 4, Berlin, Gebrüder Borntraeger, 410 pp.

WILLIAMS, E. E.
1961. Notes on Hispaniolan herpetology. 3. The evolution and relationships of the *Anolis semilineatus* group. Breviora, Mus. Comp. Zool., No. **136**: 1-8.
1965a. The species of Hispaniolan green anoles (Sauria, Iguanidae). Breviora, Mus. Comp. Zool., No. **227**: 1-16.
1965b. Hispaniolan giant anoles (Sauria, Iguanidae): New data and a new subspecies. Breviora, Mus. Comp. Zool., No. **232**: 1-7.

WILLIAMS, E. E., AND A. S. RAND
1961. Notes on Hispaniolan herpetology. 2. A review of the *Anolis semilineatus* group with a description of *Anolis cochranae*, new species. Breviora, Mus. Comp. Zool., No. **135**: 1-11.

WOODRING, W. P., J. S. BROWN, AND W. S. BURBANK
1924. Geology of the Republic of Haiti. Rep. of Haiti Dept. of Public Works, Port-au-Prince, 631 pp.

(Received 20 January 1969.)

APPENDIX

SYSTEMATICS

The synonomy of each species cites only the original description and additions to the synonomy of Cochran (1941). The data for the cited geographical range are given in Figure 1. The extreme measurements of the snakes examined are given for each metric character; the standard error for each measurement is listed in Table 2. A list of all specimens examined, their localities and color morphs, and the stomach contents listed in Table 3 are filed with the specimens at the Museum of Comparative Zoology.

UROMACER CATESBYI (Schlegel)

Dendrophis catesbyi Schlegel, 1837, Essai sur la physionomie des serpens, 2: 226 (type loc. "L'île de St. Dominque").

Uromacer scandax Dunn, 1920, Proc. New England Zool. Club, 7: 43 (type loc. Tortuga Island).

Range. Hispaniola: the coastal area north of the Cul-de-Sac Plain, the southwest peninsula of Haiti, upland valleys of the interior of the island, Île à Vache, Île de la Gonâve, and Île de la Tortue. It is sympatric with every other species in the genus.

Diagnosis. Snout 2.0 (range: 1.7-2.7) times eye diameter; scale rows at midbody 17; ventrals 167 (range: 160-180); subcaudals 183 (range: 163-205); anterior loreal absent. 254 specimens were examined: 14 AMNH, 79 ASFS, 6 BMNH, 21 FMNH, 126 MCZ, 8 USNM.

Color pattern. Green morph: dark green above, light yellow-green below, the colors meeting on the 3rd scale row; head dark green above, cream below, a light line above the eye and a dark line from the snout to the end of the head (after MCZ 64800). A few specimens have a light lateral line on the 2nd and/or 3rd scale row. The dorsal dark green varies geographically, from a dark, brownish green in western Haiti to a very light green in the eastern Dominican Republic. Specimens from Île à Vache are somewhat lighter than those from the adjacent mainland.

Gray morph: gray above, cream below, the colors meeting on the 3rd scale row; head gray-green above, cream below, a light line above the eye (after MCZ 66350). This morph has been found in 5 specimens from the Miragoâne area.

Nomenclature. Dunn (1920) defines *scandax* as "like *Uromacer catesbyi* but with 19-11 scale rows and 181 ventrals." Examining the holotype (USNM 59438), I count 17 scale rows at midbody and 180 ventrals, with 19 scales around the neck persisting to within 5 cm of midbody. A count of 19 scale rows persists for some distance down the body in six of the 254 *catesbyi* examined; there are also three typical *catesbyi* from scattered localities with ventral counts of 177, 178, and 179. Two *catesbyi* typical in scale characters (MCZ 37607, USNM 59920) have been taken from Île de la Tortue, but larger collections may reveal an endemic subspecies of *catesbyi* for which the name *scandax* would be appropriate.

UROMACER FRENATUS (Gunther)

Ahaetulla frenata Gunther, 1865, Ann. Mag. Nat. Hist., Ser. 3, 15: 94 (type loc. "not known").

Uromacer wetmorei Cochran, 1931, Proc. Biol. Soc. Washington, 44: 91 (type loc. Isla Beata).

Range. Southwest peninsula of Haiti east and north to the Cul-de-Sac Plain, Ile à Vache, Isla Beata, and the eastern coast of Barahona Peninsula. Records outside this area have been based on misidentifications (Cochran, 1941). It is sympatric with *catesbyi* throughout its range and with *oxyrhynchus* at the base of the southwest peninsula.

Diagnosis. Snout 2.6 (range: 2.1-3.0) times eye diameter; scale rows at midbody 17; ventrals 187 (range: 177-196); subcaudals 204 (range: 185-212; but AMNH 51416 has 135 and its tail appears intact); anterior loreal absent. 102 specimens were examined: 4 AMNH, 39 ASFS, 2 BMNH, 46 MCZ, 11 USNM.

Color pattern. Gray-green morph: Gray-green *frenatus* from Île à Vache are dark blue (probably green in life) above, mottled gray to gray-brown below, the colors separated by a white line on the 2nd and 3rd scale rows from four head lengths down the neck to the vent; head blue (probably green in life) above, cream below, a light line above the eye, dorsal edge of upper labials black (after MCZ 37630). The posterior extent of the white line is variable; on some specimens it fades as far anteriorly as midbody. Gray-green *f. wetmorei* from Barahona are as above, but the white line is on the 4th and 5th scale rows from the snout to one head length behind the vent (after AMNH 51421). One specimen (MCZ 43806) is not mottled ventrally and may represent a green morph, but it has been so blackened by the preservative that it is impossible to infer its color in life.

Gray morph: Mainland *f. frenatus* are finely mottled gray above and below; a trace of green on the top of the head, light green on upper labials, chin, and ventral neck (after MCZ 65530). Gray *frenatus* from Île à Vache and the type specimen of *f. wetmorei* (USNM 83891, Isla Beata) are the same as above but with the 4th and 5th scale rows very light, thus giving the appearance of a wide, dark gray dorsal stripe (after MCZ 37629).

Nomenclature. Cochran (1931) described *wetmorei* on the basis of a single specimen (USNM 83891) from Isla Beata, noting its close relationship to *frenatus.* I have re-identified 5 specimens from the Barahona mainland (MCZ 43806, AMNH 51416, 51419-21) as *wetmorei.* These additional specimens narrow the morphological distinction between *frenatus* and *wetmorei. U. f. wetmorei* has a significantly lower ventral count (180) than *f. frenatus* (189) (t=5.7, 45d.f.), although there is extensive overlap. The color patterns of *f. wetmorei* are unlike that of mainland *f. frenatus,* but are quite similar to those of *f. frenatus* from Île à Vache. Until enough specimens are available to characterize the Barahona population, I prefer conserving the name *wetmorei* to designate a subspecies of *frenatus.*

Specimens of *frenatus* from Diquini show some characteristics that might be attributed to introgression by *oxyrhynchus.* BMNH 1913.7.17.29 has a ventral count of 196; USNM 117282 has the anterior loreal scale; MCZ 8683, USNM 117282, and 117346 differ from typical *f. frenatus* in coloration, being gray with a broad stripe of gray-green down the back. Each of these specimens can be definitely identified as an aberrant *f. frenatus*, but it seems strange that all the *frenatus* from Diquini are aberrant. Recent collections from the Diquini area include no *frenatus*, but typical *frenatus* and *oxyrhynchus* are found together in the Jacmel and Miragoâne areas, and in Port-au-Prince, adjacent to Diquini, with no evidence of interbreeding. Without a larger sample, further speculation on the significance of the Diquini population seems pointless.

UROMACER OXYRHYNCHUS Duméril and Bibron

Uromacer oxyrhynchus Duméril and Bibron, 1854. Erpétologie Générale, 7: 772 (type loc. "Senegal").

Range. Hispaniola: coastal area north of the Cul-de-Sac Plain, southwest peninsula of Haiti west to Miragoâne, Ile de la Tortue, and Isla Saona. It is sympatric with *catesbyi* throughout its range, and with *frenatus* at the base of the southwest peninsula. *U. oxyrhynchus* is not known to occur with *f. wetmorei*, though Mertens (1939: 79) reports seeing an *oxyrhynchus* and a *frenatus* in the same bush at "Camberlen" (near San Cristóbal, D.R.); he did not catch the *frenatus*, however, so that it is not possible to be sure that the snake was not a gray *oxyrhynchus.* One specimen of *oxyrhynchus* (USNM 75927), collected by J.S.C. Boswell in 1928, is reported as taken from Anse à Galets, Gonâve. Exceptional localities of other specimens in Boswell's 1928 collection have been attributed to labeling errors (Schwartz, 1965). Collections from Ile de la Gonâve in the last ten years contain many *catesbyi* and *dorsalis*, but no *oxyrhynchus.*

Diagnosis. Snout 3.0 (range 2.5-3.7) times eye diameter; scale rows at midbody 19; ventrals 200 (range: 189-212); subcaudals 199 (range: 183-211); anterior loreal present in 25 of the 129 specimens examined: 6 AMNH, 8 BMNH, 2 FMNH, 97 MCZ, 15 USNM, 1 YPM.

Color pattern. Green morph: dark green above, light yellow-green below, the colors separated by a white lateral line on the 1st and 2nd scale rows from the snout to two headlengths beyond the vent, ventral edge of the scales in the 1st row black; head green above, cream below, a light line above the eye, dorsal edge of upper labials black (after MCZ 62701). There are variations in color intensity. The lateral line may be edged by black, yellow, both, or neither. In a few specimens, as much as the anterior half of the lateral line is indistinct or lacking.

Gray-green morph: like the green morph, but with the ventral surface finely mottled gray to gray-brown from the neck to the tip of the tail (after MCZ 62703). This morph has been found in Haiti and in the eastern Dominican Republic. Variations are as in the green morph.

Gray morph: finely mottled gray above, more coarsely mottled gray below, 2nd, 3rd, and 4th scale rows lighter gray, dorsal edge of scales in the 5th row black from midbody to vent; head as in the green morph (after MCZ 62702). Four specimens of this morph have been taken from scattered localities in Haiti.

UROMACER DORSALIS Dunn

Uromacer dorsalis Dunn, 1920, Proc. New England Zool. Club, **7**: 43 (type loc. Gonave Island).

Range. Île de la Gonâve. It is sympatric with *catesbyi.*

Diagnosis. Snout 2.9 (range: 2.5-3.7) times eye diameter; scale rows at midbody 17 (19 in MCZ 93146); ventrals 200 (range: 192-210); subcaudals 210 (range: 197-228); anterior loreal present (absent in MCZ 93139). 84 specimens were examined: 7 ASFS, 65 MCZ, 12 YPM.

Color pattern. The species is monomorphic: finely mottled gray above and below, the dorsal region between the 5th scale rows darker; head green above, light green below (after MCZ 61043). In very light specimens the dorsal stripe is indicated only by black spots on the dorsal edge of scales in the 4th row.

Nomenclature. U. dorsalis is more similar to *oxyrhynchus* than to *frenatus* in general body form, snout length, ventral count, and the presence of the anterior loreal scale, but more similar to *frenatus* in midbody scale count, subcaudal count, and color pattern. Since *dorsalis* is unique in its diet and morphologically intermediate between two distinct mainland species, I retain it as a distinct species. Although I admit a close relationship between *dorsalis* and *oxyrhynchus,* the evidence is not compelling enough to warrant calling *dorsalis* a race of *oxyrhynchus.*